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PHYLOGENY OF THE RACES OF VOLUTILITHES PETROSUS.

BY BURNETT SMITH, PH.D.

INTRODUCTION.

In a recent article¹ the author has described some of the shell characters which, occurring in the later stages of Gastropod ontogeny and phylogeny, mark the gerontic or senile condition of the individual or of the race. It was seen that these senile features may at times be as useful to the student of phylogeny as those of the earlier stages, which latter have always received the more attention. In the paper referred to, the attempt was made to show that the modern *Fulgur carica* of our New Jersey coast is the descendant of a main *F. carica* stock, which originated in Miocene time; and that such forms as *F. maximum* and its allies, which had heretofore been regarded as ancestral by Grabau² and others, are in reality not so at all, but senile offshoots which at an early period in the history of the stock diverged from the main line of descent. The paucity of individuals representing the forms considered ancestral, and the extreme abundance of the specimens of senile forms, was a source of some embarrassment to the author. It is therefore with considerable satisfaction that I am now able, though in another genus (*Volutilithes*), to present a series in which the forms comprising the main ancestral stock are nearly as plentiful as those which represent the senile offshoots.

The history of certain of the species of *Volutilithes* can be well traced in the Eocene of our Gulf States, but nowhere better than in Alabama, where the fine sections along the Alabama and Tombigbee rivers have furnished abundant material for the study of the geological and geographical distribution of these forms. The races and species studied range from the Matthew's Landing horizon in Alabama to the Jackson horizon in Mississippi, and therefore represent a fair proportion of the phylogenetic units through nearly the whole of the Eocene. They are likewise restricted to a small geographical area, and the geological sections in which they appear are unusually good.

¹ Senility among Gastropods, *Proc. Acad. Nat. Sci. Phila.*, May, 1905.

² Studies of Gastropoda, II—*Fulgur* and *Sycotypus*, *Am. Nat.*, Vol. 37.

The material at my disposal is very full and complete,³ and has enabled me to study large series of individuals. These series in each case represent the forms in the proportions in which they occur in the field, and therefore offer every opportunity for obtaining the average racial characters in any particular locality or horizon.

MORPHOLOGY.

The genus *Volutilithes* is widely distributed throughout our Southern Eocene. At some localities several sharp and distinct species occur, but at most of the localities *Volutilithes* is represented by one species and by a particular race of that species. The term race is used in place of variety, for in these assemblages the individuals frequently differ widely. There is, however, always an average of characters which stamps the stage of evolution which the race has attained. Of course, extreme specimens often have more of the features of some other race than of the race to which they belong, but these individuals are always few; and there is never any difficulty in recognizing the general race characters for any particular geographical point, and the phase of phylogenetic development found in the faunule at that point. In cases of this sort, the introduction of varietal and specific names is to be deprecated, and the adoption of the system of race analysis is strongly urged by the author.

In the forms under consideration, the first two or three whorls are smooth and rounded, constituting the Smooth Stage. The first ornamental feature to appear on the smooth, rounded whorl is the transverse rib, that is, a slight elevation on the whorl which runs across it from suture to suture. These early ribs are invariably curved slightly, and each one is simple and uniform from suture to suture. The curved ribs persist as a rule for about a quarter or a half of a whorl, or even for a much less space; in fact, sometimes we have only one or two of them. This Curved Rib Stage is short but remarkably constant, and though occasionally much suppressed, has been found in every species and race dealt with in this paper.

The curved ribs, after about one-third of a whorl, change abruptly into the straight ribs of what has been designated the Cancellated⁴

³ It forms part of the Isaac Lea Collection of Eocene Mollusca at the Academy of Natural Sciences of Philadelphia, and was brought together largely by Mr. Charles W. Johnson, now of the Boston Society of Natural History. The collections are a tribute to his skill and perseverance as a collector, and are an example of what museum research collections should be.

⁴ See Dall, *Trans. Wag. Inst.*, Vol. III, p. 68.

Stage, which begins by the appearance of two swellings or tubercles on each rib. One of these tubercles is near the suture, and the other at the position which is later occupied by the shoulder angle. They will be referred to as the suture and shoulder tubercles respectively. These two tubercles are often of nearly equal size at the start, though frequently the suture tubercle is the larger. Tubercles other than these two mentioned are seldom visible on an early rib; but when a sufficiently small shell is obtainable, other smaller tubercles can be seen upon each rib, and the tubercles diminish in size quite regularly from the suture tubercle downward. Each tubercle is connected with the corresponding tubercle of the next rib by a faint spiral, the first appearance of the definite cancellation which later becomes more pronounced. In most specialized forms the shoulder angle develops shortly after the appearance of the tubercles.

The cancellated condition is found more or less well developed in all the different races. In primitive species ⁵ it may persist as a constant feature to the end of the individual's life; but in most forms it covers only a few whorls and is more variable than the preceding Curved Rib Stage, in that certain of its features change as the shell grows. These changes are gradual, but they render the end of the Cancellated Stage much less definite than its beginning. They may be briefly summarized as follows: The tubercles, with the exception of the shoulder tubercle, usually tend to degenerate, and soon disappear, though their corresponding faint spirals may sometimes persist.

The shoulder tubercle, on the contrary, becomes stronger and sharper. First the ribbing above the shoulder disappears, and later the ribbing below the shoulder shortens, and with its practical disappearance what might be termed the Spiny Stage is inaugurated.

In the Spiny Stage the shoulder tubercle is now sharp and spine-like. Other tubercles have disappeared and the spirals are, as a rule, restricted to the region of the anterior siphon. Ribbing has practically gone, but very short rudiments may sometimes still be present below the shoulder spines. The commencement of this stage is never sharp, for it is the result of gradual change from the preceding one.⁶ It is

⁵ In *Am. Nat.* for 1902, Vol. 36, p. 926, Grabau says: "It is perhaps not too much to say that in the majority of the larger phyletic series, except those highly specialized, the radicle is a smooth, round-whorled form, succeeded by types in which the adults are ribbed, and later cancellated, after which progressive modification may be carried further."

⁶ No morphological distinction is made between spine and tubercle. "The writer considers that the difference between the small rounded tubercle of the early whorls and the large, sharp spine of the later whorl is one merely of degree.

not reached in all species, but occurs usually as the end term of normal progressive development in the ontogeny, and of slow and even evolution in the phylogeny.

The Spiny Stage, then, may sometimes be present as a well-defined stage, but it may also be accompanied by extreme individual variation and by features of senility. These latter characterize the Senile Stage, and may follow regularly after the Spiny Stage; but, as stated above, they not infrequently are thrown back by acceleration, and found together in the same whorl with the features of the Spiny Stage.

The Senile Stage, whether following normally after the Spiny Stage or associated with it, is always easily distinguished. In the forms under consideration its most important features are the following: ⁷

1. Tendency for the shoulder spines to pass into a shoulder keel.
2. Irregularity of growth lines.
3. Thickening of the shell.
4. Encroachment of the anal siphon upward on the preceding whorl.
5. Protrusion of the mantle in the region of the anal siphon, producing a smoothing of the preceding whorl by a shelly overgrowth.

These five characters are all sometimes found together in one individual or race, but, as a rule, only two or three of them are so associated.

In studying the development of the shell features, each whorl has been taken up in detail, and its particular ornamental characteristics noted. Of course, this system is more or less arbitrary, and at times

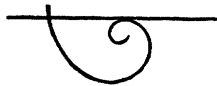


Fig. 1.—Line shows position taken for the end of the first whorl.

inaccurate, on account of the acceleration of features in certain individuals. In the following study, the writer has endeavored to get the average characters for a certain whorl, except where individual variation is great. In this latter case the variations are noted.

The word spine is therefore used, throughout this paper, simply in a descriptive sense, and implies no difference from the early tubercle, except that it is larger and sharper. Both are produced by the same fold in the mantle, and every gradation between the two is observable." Smith, Burnett, *Proc. Acad. Nat. Sci. Phila.*, May, 1905, p. 347. This opinion is quite different from that held by Grabau (see *Am. Nat.*, Vols. 36, 37).

⁷ For a discussion of senility see Smith, Burnett, *Proc. Acad. Nat. Sci. Phila.*, May, 1905.

In counting the whorls, it has been attempted to have the end of the first whorl come in about the position shown in the figure. It is impossible to make an absolutely exact count, but if care is used there will seldom be much of an error in the last whorl. As stated above, the method is purely arbitrary, but it seemed to the writer to be the only practical way in which the statistics of the development of ornamental features could be arranged.

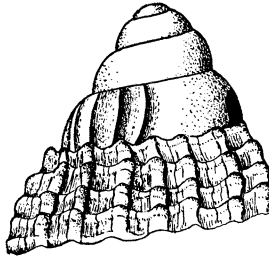


Fig. 2.—*Volutilithes limopsis* Conrad. Matthew's Landing, Ala. Apex enlarged, showing smooth stage followed by the curved rib stage, which begins in the latter part of whorl four. Whorl five shows the cancellated stage. Length = 1.6 mm.

***Volutilithes limopsis* Conrad.**

Locality—Matthew's Landing, Ala.

This species was originally described by Conrad in *Jour. Acad. Nat. Sci. Phila.*, 2d Series, Vol. IV, p. 292, Pl. 47, fig. 24.

Whorls 1, 2, 3—Smooth and rounded.

Whorl 4—Smooth and rounded, except toward the end, where the curved rib stage may start.

Whorl 5—The curved rib stage often commences early in five, persisting as a rule for about a quarter of a whorl. The cancellated stage follows abruptly with its straight, tubercled ribs. These tubercles are largest at the suture, decreasing regularly in size anteriorly on each rib. Each tubercle is connected with the corresponding tubercle of the next rib by a faint spiral. A shoulder angle is never developed.

Whorls 6, 7—Characterized by the cancellated stage and much like the latter part of five.

Whorl 8—Characterized by the cancellated stage and much like six and seven. The tubercles nearest the suture are the strongest, and they diminish in size regularly as the rib is followed anteriorly. The ribs are also less prominent anteriorly, disappearing entirely on the branchial siphon. Spirals cover the entire whorl.

Whorls 9, 10—Much as in eight, the cancellated stage still persisting.

The tubercles are a little sharp, and the protruded mantle shows a very slight tendency to smooth the preceding whorl—a tendency which in later forms results in a senile feature.

Remarks.—This form possesses no stage later than the cancellated stage and never has a shoulder angle. The suture tubercle is throughout life the dominant one. The specimens are remarkably uniform, no perceptible individual variation occurring. The smooth stage is very long. From its primitive characteristics, and its geological position near the base of the Eocene, the writer has no hesitation in assigning to it an ancestral position among the races and species dealt with in this paper.

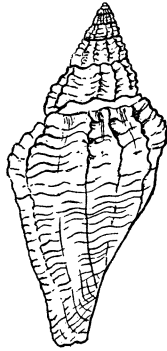


Fig. 3.—*Volutilithes rugatus* Conrad. Matthew's Landing, Ala. Adult individual. Length=44 mm.

***Volutilithes rugatus* Conrad.**

Locality—Matthew's Landing, Ala.

This species was originally described by Conrad as *Volutilithes rugata* in *Jour. Acad. Nat. Sci. Phila.*, 2d Series, Vol. IV, p. 292, Pl. 47, fig. 32.

Whorls 1, 2, 3—Smooth and rounded.

Whorl 4—Smooth and rounded, except near the end, where in many individuals the curved rib stage begins.

Whorl 5—The curved rib stage usually occupies the latter part of four and early part of five. Its ribs are wide apart and it persists for about a quarter of a whorl. It is followed by the straight, tubercled ribs of the cancellated stage. The two upper tubercles are the largest, those below becoming fainter anteriorly. The ribs die away anteriorly on the branchial siphon. Each tubercle is connected with the corresponding one of the next whorl by a spiral.

Whorls 6, 7, 8—All characterized by the cancellated stage. Changes, however, take place during these whorls. At first the ornamentation is much like that of the cancellated stage in *V. limopsis*, but later the ribs become relatively farther apart and broader (in a spiral direction). At the same time many fine riblets are introduced between the primary ribs. The tubercles are largest near the suture and become smaller as the ribs die away anteriorly. There is never a distinct shoulder angle. The whorls are covered with spirals.

Whorl 9—Individual variation now sets in. In some specimens the whorl is much as in eight. In others the rib is swollen into a very rounded, transversely long angle which hardly occupies the position of the shoulder angle of later forms, and in addition the shells become thick. In all individuals the mantle protrudes in the region of the anal siphon, and tends to smooth the preceding whorl with a shelly overgrowth. This latter is never extreme.

Whorl 10—Much as in nine, though here the forms with swollen ribs predominate. In many specimens the shells become thick, the growth lines irregular, and the smoothing of the preceding whorl by the shelly overgrowth is quite well marked, though it never becomes extreme as in some forms of later time.

Remarks.—This species in its earlier stages of growth closely resembles *V. limopsis*. It differs radically, however, from that form with the progress of its ontogeny. Though its individuals vary greatly, it is nevertheless entitled (in the opinion of the author) to rank as a distinct species. In its later whorls there is great individual variation, accompanied by senile features. These latter, though never extreme, are well marked. They comprise protrusion of the mantle in the region of the anal siphon, producing a smoothing of the preceding whorl by a shelly overgrowth; thickening of the shell, and irregularity of growth lines. There is no spiny stage. *V. rugatus* is considered to be a short senile offshoot from *V. limopsis*. In the absence of intermediate forms this evolution must have taken place either at some other locality or at some geologically earlier date.

***Volutilithes petrosus* Conrad.**

The forms described at the present day under this name represent an assemblage of races. If every gradation of evolutionary development did not exist among them, many of these races would doubtless now be regarded as distinct species. In fact, there are several discarded specific names which were used in this way by Conrad and Lea. Each race is an assemblage of individuals, showing more or less in-

dividual variation, yet nevertheless possessing on the average definite racial characters. In other words, the majority of specimens from any one locality or horizon show a certain stage of evolution. Some of the specimens may show developmental features characterizing either a more primitive or a less primitive race; but these specimens are few, and are not typical of the average of individuals from the locality or horizon to which they belong.

The races of *V. petrosus* are known to range from the Nanafalia beds to the Jackson beds inclusive. The original specific description⁸ is accompanied by a figure of a member of the Claiborne race. Though this particular race is perhaps not the most typical expression of the *V. petrosus* main stock, the writer feels that no better method can be employed than to use the name *V. petrosus* to designate the assemblage of races under discussion.

Several of the races differ in the development of senile characters from the *V. petrosus* main stock, but there is every gradation between these and the representatives of the main stock. On account of this gradation the senile forms are included as races of *V. petrosus*, in spite of the fact that their old individuals differ greatly in appearance from those of the more normal type.

The young of all the races, senile and otherwise, are remarkably uniform and constant. The early whorls indicate clearly that they are all descended from a cancellated ancestor, and bear a strong resemblance, especially in the cancellated stage, to the characters of *V. limopsis*. In the absence of any record of a *V. petrosus* being found below the horizon of the Nanafalia beds, the author believes that it is perfectly safe to conclude that all these races in question are descended from the *V. limopsis* of the Matthew's Landing horizon.

***Volutilithes petrosus* Conrad.**

Nanafalia Race.

Locality—Nanafalia, Ala.

The only specimen known to the writer from this horizon is not sufficiently well preserved to admit of its accurate study whorl for whorl. It is, however, a perfectly normal specimen of moderate size and expresses the general characters of the *V. petrosus* main stock. It is about the size of the eight-whorled individuals of the Gregg's Landing or the Jackson races. When it is placed in line with such specimens, the three shells exhibit very few differences. This Nanafalia individual

⁸ *Voluta petrosa* Conrad, "Fossil Shells of the Tertiary Formations of North America."

has spines in its last whorl which make it resemble the Jackson race quite closely. In this respect it is nearer the Jackson specimens than the Gregg's Landing specimens. Its mantle perhaps smooths the preceding whorl a trifle more than does the mantle in the Jackson race. However, in its general features, it is very close to the Jackson form. The amount which the mantle has smoothed the preceding whorl is about equal to that found in shells of the same size from Gregg's Landing.

***Volutilithes petrosus* Conrad.**

Gregg's Landing Race.

Locality—Gregg's Landing, Alabama River, Ala.

Whorls 1, 2, 3—Smooth and rounded.

Whorl 4—The curved rib stage begins early in four. It persists for a quarter or a third of a whorl, but changes abruptly into the cancellated stage with its straight, tubercled ribs. The shoulder and suture tubercles are of about the same size at first. By the end of four the shoulder angle is quite well developed.

Whorl 5—Characterized by the cancellated stage and much like the latter part of four. Suture and shoulder tubercles are of about the same size. The shoulder angle is well developed. Tubercles are connected by fine spirals.

Whorl 6—Characterized by the cancellated stage, but changes occur. The shoulder tubercle is becoming stronger, while the suture tubercle is getting weaker. The ribbing above the shoulder angle is also becoming weaker.

Whorl 7—Still characterized by the cancellated stage, but here the suture tubercle has disappeared and is only represented by its spiral. The ribbing above the shoulder angle has gone, though it is still well represented below the shoulder angle.

Whorl 8—Still characterized by the cancellated stage and much like whorl seven. Below the shoulder angle the whorl is covered with fine spirals. There is a very slight smoothing of the preceding whorl by the protruded mantle, for the end of the cancellated stage is not sharp like that of the curved rib stage.

Whorl 9—From here on individual variation is great. Some forms have a whorl much as in eight, with the ribbing still well developed below the shoulder, though the shoulder tubercles are more spine-like. In other specimens the ribbing below the shoulder is gone, the shoulder spines are more extreme, and the anal siphon shows a tendency to encroach upward on the preceding whorl. In addition, these

latter forms have a heavier shell, and the shelly smoothing of the preceding whorl by the protruded mantle is more marked.

Whorl 10—Here again we have every gradation between forms characterized by the spiny stage, in which the preceding whorl has been only slightly smoothed by the mantle, and forms which show a moderate development of senile features. These latter show the tendency for the spines to pass into a shoulder keel. They also possess a thick shell with irregular growth lines, the anal siphon encroaches upward, and the preceding whorl is smoothed by the shelly overgrowth of the protruded mantle. Though these latter forms possess senile features, these features are only slightly developed. They are, in fact, just the beginnings of those characteristics which become so extreme in some of the races of later time.

Remarks.—This race occurs in the Gregg's Landing marl. The greater number of individuals of the Gregg's Landing race have a perfectly normal ontogeny, and in their later whorls have the spiny stage well marked. These individuals belong therefore to the *V. petrosus* main stock, and as they form a majority of the assemblage, they determine the position of the race to be on the main stock. A minority of individuals, however, show senile features. These senile features are not well marked, but they indicate that here in this race was inaugurated the tendency which resulted in the development of the senile races of later time. In other words, we have here the point where a senile offshoot is starting to branch from the main ancestral stock. The marks of this tendency are but slight, and the individuals are few; yet, nevertheless, the tendency is plainly recognizable.

Volutilithes petrosus Conrad.

Bell's Landing Race.

Locality—Bell's Landing, Alabama River, Ala.

Whorls 1, 2, 3—Smooth and rounded.

Whorl 4—The curved rib stage commences early in four and persists for about a quarter of a whorl. It is followed by the straight, tubercled ribs of the cancellated stage. The suture and shoulder tubercles are about equal in size, and the shoulder angle soon becomes well marked. Spirals connect the tubercles.

Whorl 5—Characterized by the cancellated stage and closely resembles the latter part of four.

Whorl 6—Characterized by the cancellated stage. Suture tubercles grow weaker, shoulder tubercles grow stronger. Ribbing above the shoulder also grows weaker, but it is well marked below the shoulder.

Whorl 7—Much as in six.

Whorl 8—Still characterized by the cancellated stage, but the suture tubercles and the ribbing above the shoulder have now gone. Shoulder tubercles are stronger. Ribbing below the shoulder is weaker. The beginning of the tendency to form a shelly overgrowth is seen, and the cancellated stage comes to an end.

Whorl 9—Ribbing is about gone and the shoulder tubercles have become spines. In other words, the spiny stage has set in. In most individuals, however, the senile characters are also mingled with those of the spiny stage. The shell gets thicker, and the mantle protrudes in the region of the anal siphon, and smooths the preceding whorl with a shelly overgrowth. This latter, though not extreme, often covers the spines of eight, which, however, are visible through it.

Whorls 10, 11, 12—In these whorls we simply have an exaggeration of the characters of nine. The features of the spiny stage and the marks of senility are found together in the same whorl. Toward the end senile characters are quite well marked. The shell becomes thick, the growth lines irregular, the anal siphon encroaches upward, and the shoulder spines tend to pass into a shoulder keel. In addition, the shelly overgrowth produced by the protruded mantle is well marked, and in some specimens may be quite thick. As a rule, however, the spines of the preceding whorl can be counted through the shelly envelope.

Remarks.—This race occurs in the Bell's Landing marl. Though occasionally a rare specimen may nearly approach the *V. petrosus* main stock in its general features, the vast majority of individuals show such a development of senile characters that it is necessary to consider the race to be a senile offshoot from the main stem. These senile marks though typical are not highly developed. This race unquestionably sprang from the senile individuals which occurred as a minority in the otherwise normal, geologically earlier Gregg's Landing race.

***Volutilithes petrosus* Conrad.**

Wood's Bluff Race.

Locality—Wood's Bluff, Tombigbee River, Ala.

Whorls 1, 2, 3—Smooth and rounded.

Whorl 4—The curved rib stage appears early in four and persists for about a quarter of a whorl. It is followed by the straight, tubercled ribs of the cancellated stage. The suture and shoulder tubercles are about equal in size. A shoulder angle soon develops. The tubercles are connected by spirals.

Whorl 5—Characterized by the cancellated stage and closely resembling the latter part of four.

Whorl 6—Characterized by the cancellated stage. Ribbing above

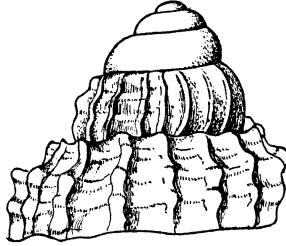


Fig. 4.—*Volutilithes petrosus* Conrad. Wood's Bluff Race. Wood's Bluff, Ala. Apex enlarged. The first three whorls are characterized by the smooth stage. In whorl four the passage from the curved rib stage to the cancellated stage can be seen. Whorl five shows the cancellated stage. It will be noted that the stages are all more accelerated than in text fig. 2. Length = 1.5 mm.

the shoulder growing weaker, though well marked below the shoulder. Suture tubercles weaker, shoulder tubercles stronger.

Whorl 7—Much as in latter part of six.

Whorl 8—Still characterized by the cancellated stage, but the suture tubercles are gone, and are represented only by their spiral. Ribbing above the shoulder has disappeared, though it is still present below the shoulder. The ribbing below the shoulder is, however, weaker. The tendency to form a shelly overgrowth is plainly seen. Though its end is not well marked, the cancellated stage comes to a close with this whorl.

Whorl 9—The spiny stage usually begins with this whorl. It is, however, accompanied by well-developed senile features, the most marked of which is the shelly overgrowth, which is produced by the protrusion of the mantle on to the preceding whorl.

Whorls 10, 11, 12—Here we have simply an exaggeration of what occurs in nine. The shelly overgrowth is extreme, obscuring the ornamentation of several of the earlier whorls. The shell becomes thick, the growth lines irregular, the anal siphon encroaches upward, and the shoulder spines tend to pass into a shoulder keel.

Remarks.—This is typically a senile race. No individuals of more than eight whorls ever approach in their general appearance the *V. petrosus* main stock. All specimens exhibit senile characters. These latter are much more extreme than those found in the geologically

earlier Bell's Landing race. It has unquestionably been evolved from the Bell's Landing race by an exaggeration of senile characters.

***Volutilithes petrosus* Conrad.**

Hatchetigbee Bluff Race.

Locality—Hatchetigbee Bluff, Tombigbee River, Ala.

The series of young individuals at hand is so small, and the shelly overgrowth produced by the protruded mantle is so great in the old individuals, that a detailed study of the specimens, whorl for whorl, is not practical.

These forms are extraordinarily senile, and have been derived from the geologically earlier Wood's Bluff race by an exaggeration of the senile features. The shoulder spines tend to pass into a shoulder keel, the shell is thick, the growth lines irregular, the anal siphon encroaches upward, and the preceding whorl is encumbered with the shelly overgrowth. This last feature is very extreme. In addition the race is, on the whole, a dwarfed race, the full-grown individuals being smaller than those of the earlier less senile races. This race is the end term of the senile offshoot which diverged from the *V. petrosus* main stock in Bell's Landing time. The author knows of no authentic abnormal senile specimen from beds higher than the Hatchetigbee horizon in Alabama or Mississippi.⁹

***Volutilithes petrosus* Conrad.**

Yellow Bluff Race.

Locality—Yellow Bluff, Alabama River, Ala.

Unfortunately the material at hand is not sufficiently well preserved to give a detailed description, whorl for whorl. Nevertheless, there is no difficulty in making out the following points. The great majority of individuals possess, in general, the characters of the *V. petrosus* main stock, and have arrived at little more than that evolutionary stage which is typified by the Gregg's Landing race.

Though a few individuals exhibit senile characters, these latter are only very slightly developed, and we are undoubtedly warranted in placing the Yellow Bluff race on the *Volutilithes petrosus* main stock as the descendant of the Gregg's Landing race.

The exact stratigraphical horizon for this race is unknown to the

⁹ See *Trans. Wag. Inst.*, Vol. III, part 1, p. 75. The statement made on this page by Dall is not borne out by a study of full collections. He says that *Athleta* "is foreshadowed by the distorted specimens of *Volutilithes petrosa* to which I have already referred, and which occur from the Lower Eocene of Alabama (Wood's Bluff) up to the Claiborne Sands and the beds known as Jackson, overlying the Claiborne, associated with the undistorted normal form, which is always more numerous."

author. It cannot, however, be lower than that of the Bell's Landing marl. If it is at the same horizon, we have an example of a slightly senile race (the Bell's Landing) living at the same period of time not far from a race (the Yellow Bluff) which exhibits, on the whole, main stock characteristics. If, on the other hand, the Yellow Bluff race occupies a position above the Bell's Landing marl, we have a primitive race overlying a more specialized race. If this latter is the case, a discordance between the geological and phylogentic successions has been produced by the migration into the section of the Yellow Bluff race.

***Volutilithes petrosus* Conrad.**

Lower Claiborne Horizon, Claiborne, Ala.

Very poorly preserved specimens are found in these beds. They are determinable as representatives of the *V. petrosus* main stock, but a detailed study, whorl for whorl, is not practical.

***Volutilithes petrosus* Conrad.**

Claiborne Race.

Locality—Claiborne, Ala.

Whorls 1, 2, 3—Smooth and rounded.

Whorl 4—Early in four the curved rib stage appears. It is not well marked, persisting for but a short time, and is soon followed by the straight, tubercled ribs of the cancellated stage. The shoulder angle soon develops. The suture and shoulder tubercles are of about the same size.

Whorl 5—Characterized by the cancellated stage and much as in the latter part of four. Spirals not strong. Suture tubercle weakens, shoulder tubercle becomes stronger.

Whorl 6—Characterized by the cancellated stage. The suture tubercle and the ribbing above the shoulder are almost gone. Shoulder tubercle stronger. Ribbing below shoulder is weaker.

Whorl 7—The ribbing and the suture tubercles disappear, and the shoulder tubercles develop into spines during this whorl. In other words, we have the transition from the cancellated to the spiny stage.

Whorls 8, 9, 10—All characterized by the spiny stage, but individual variation is great. Senile features do not appear.

Remarks.—Occurs in the Claiborne Fossiliferous Sand. This race exhibits in general the characters of the *V. petrosus* main stock, though it is probably not the most typical expression of that stock as it existed at the time of the Claiborne deposits. The most notable features are the shortening of the curved rib stage and the acceleration of the spiny

stage, which is long and well developed though accompanied by considerable individual variation. The curved rib and cancellated stages are very short.

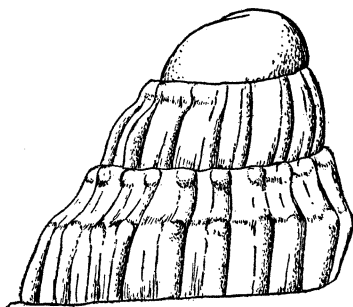


Fig. 5—*Volutilithes sayana* Conrad. Claiborne, Ala. Apex enlarged, showing ornamental features thrown far back by acceleration. The smooth stage is almost entirely confined to the large first whorl. In whorl two the transition from the straight untubercled ribs (suppressed curved rib stage) to the cancellated stage is seen. Whorl three shows the cancellated stage. Length = 1.8 mm.

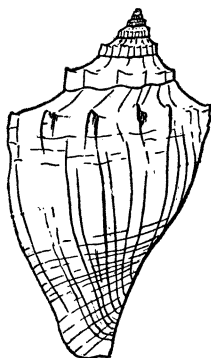


Fig. 6.—*Volutilithes sayana* Conrad. Claiborne, Ala. Adult individual. Length = 48 mm.

***Volutilithes sayana* Conrad.**

Locality—Claiborne, Ala.

This species was originally described as *Voluta sayana* by Conrad.¹⁰

Whorl 1—Smooth and rounded.

Whorl 2—Smooth and rounded at first, but soon ribbing begins. Untubercled ribs are the first ribs, but they are not curved. Neverthe-

¹⁰ *Fossil Shells of the Tertiary Formations of North America.*

less they probably represent the curved rib stage and will be assigned to it. They persist for only a short while and are followed by the tubercled ribs of the cancellated stage. At first the suture tubercle is considerably larger than the shoulder tubercle. A shoulder angle soon develops, and by the end of the whorl the suture and shoulder tubercles are about of the same size.

Whorls 3, 4—Characterized by the cancellated stage and much as in latter part of two. Changes however occur, for the ribbing above the shoulder and the suture tubercles weaken, though the shoulder tubercle becomes stronger. The spirals are not well marked.

After whorl four great individual variation sets in. The cancellated stage may persist through the sixth whorl. After this the individual variation is still more marked. Many specimens pass through the spiny stage, though it is considerably modified by the development of numerous secondary spirals and riblets. In many specimens the shoulder spines are long in a transverse direction and notched by several spirals. Sometimes the whorl may be of a rounded shape, with the spines blunt, weak and obscure.

Remarks.—Occurs in the Claiborne Fossiliferous Sand. This most variable species has an apex very different from those of the other forms considered in this paper. The smooth stage is nearly all confined to the first whorl, which is extraordinarily large for *Volutilithes*. By a careful study of its ontogeny it is plain, however, that this species was derived by acceleration from the Claiborne race of *V. petrosus*, or else from some form very close to it. We are forced, then, to the conclusion that shells with rather different apices may sometimes be very nearly related; in spite of the fact that, as a rule, this condition precludes close affinity. Though this variable species may have given rise to species and races of later age than the Claiborne, the writer has no evidence to that effect. The anal siphon does not encroach upward, and the protruded mantle smooths the preceding whorl but little; nevertheless, the thickness of the shell and the irregularity of growth lines in many of the older individuals point to the fact that it is a senile race. It is well developed in the Claiborne horizon at several points, where it is always variable and more numerous than the Claiborne race of *V. petrosus*. From this latter race it was probably evolved during or just before Claiborne time, and may therefore be considered as a senile offshoot from the *V. petrosus* main stock.

Volutilithes petrosus Conrad.

Jackson Race.

Locality—Jackson, Miss.

An individual of this race was originally described by Conrad as *Volutilithes symmetrica*.¹¹

Whorls 1, 2—Smooth and rounded.

Whorl 3—The curved rib stage commences early in three and persists for about a quarter of a whorl. It is followed by the straight tubercled ribs of the cancellated stage. The suture and shoulder tubercles are about equal in size. By the end of the whorl the shoulder angle is well marked.

Whorls 4, 5—Characterized by the cancellated stage. Ribbing above the shoulder weakens, as does also the suture tubercle. Shoulder tubercle gets stronger. Ribbing below the shoulder well marked and crossed by fine spirals.

Whorl 6—Characterized by the cancellated stage and much as in five.

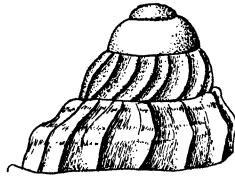


Fig. 7—*Volutilithes petrosus* Conrad. Jackson Race. Jackson, Miss. Apex enlarged. Whorls one and two show the smooth stage. Whorl three shows the curved rib stage and whorl four the cancellated stage. It will be noted that the stages are all more accelerated than in text fig. 4, but less accelerated than in text fig. 5. Length = 1.3 mm.

Whorl 7—Characterized by the cancellated stage. Ribbing gone above the shoulder, but well developed below the shoulder, and crossed by fine spirals. Suture tubercles almost gone though represented by a spiral. Shoulder tubercle stronger and sharper.

Whorl 8—Much like seven, but toward the end the ribs disappear, the shoulder tubercle becomes a spine, and the cancellated stage comes to a close.

Whorl 9—Characterized by the spiny stage. High shoulder spines and no ribs. Spirals well developed, but strongest on the anterior siphon.

Whorl 10—In many individuals the shoulder spines tend to pass into a shoulder keel, the shell thickens, and the growth lines become irregular. The shelly smoothing of the preceding whorl by the protruded mantle is only slight. This whorl is characterized by the senile stage.

¹¹ *Proc. Acad. Nat. Sci. Phila.*, Vol. VII, p. 260. In this case "*Volutilithes*" is probably a typographical error.

Remarks.—This race shows a regular and even ontogeny. The different stages are quite distinct. The senile characters are not thrown back into the spiny stage but follow regularly after it, and constitute the culminating feature of individual development. These marks of old age are never extreme. Acceleration early in life has placed the curved rib stage at the beginning of the third whorl, and the cancellated stage has been correspondingly lengthened. The cancellated stage is longer here than in any of the other forms considered in this paper except *V. limopsis*. This assemblage is the last representative of *Volutilithes* in the Alabama and Mississippi Eocene. It fulfills every requirement for position on the *V. petrosus* main stem, it is the culminant race of the stock, and has attained its characters by a slow and even phylogenetic development.

***Volutilithes haleanus* Whitfield.**

Locality—Lisbon, Ala.

Whorls 1, 2—Smooth and rounded.

Whorl 3—Smooth and rounded at first, but later the curved rib stage begins. This persists for about a quarter of a whorl, and is then followed by the straight, tubercled ribs of the cancellated stage. The shoulder tubercle is just a trifle larger than the suture tubercle. The shoulder angle is well marked by the end of the whorl.

Whorl 4—Characterized by the cancellated stage. Shoulder angle. Shoulder tubercle stronger than the suture tubercle.

Whorls 5, 6—Characterized by the cancellated stage and much like whorl four. During these whorls the suture tubercle tends to attain the same strength as the shoulder tubercle. Spirals not very well marked.

Whorl 7—From here on the primitive cancellated stage is replaced by what may be called a modified cancellated stage. The suture and shoulder tubercles are now of about the same size. The ribs are crowded so closely together that they are almost in contact, being separated by a mere depressed line. The shoulder tubercles are so close together that the general effect is that of a whorl with a shoulder keel.

Whorls 8, 9—Much as in seven, but toward the end the shell becomes thick and the growth lines slightly irregular. The protruded mantle produces only an insignificant smoothing of the preceding whorl.

Remarks.—By a study of its early whorls it is evident that this form was at some time derived from the *V. petrosus* main stock. Its cancellated stage closely resembles that of the races of *V. petrosus* until we reach the seventh whorl. After that it is quite different in its general

characters from every other American species of *Volutilithes*. Just when it diverged from the *V. petrosus* main stock the writer is not prepared to say. This race has, properly speaking, no senile stage.

In order to show more clearly some of the important correlations between the ontogeny and phylogeny, the following tables are introduced. The figures stand for the number of the whorl, while the letters are used for the different ontogenetic stages as follows:

A—Smooth Stage.

B—Curved Rib Stage.

C—Cancellated Stage.

D—Spiny Stage.

E—Senile Stage.

I—Individual Variation.

This last may appear anywhere, but it usually follows stage C. B is exaggerated in all the tables.

	1	2	3	4	5	6	7	8	9	10	11	12	
<i>V. limopsis</i> . Matthew's Ldg.			A	B _I				C					
<i>V. petrosus</i> . Gregg's Ldg. Race.		A		B _I		C			D and I				E. is very slight.
<i>V. petrosus</i> . Jackson Race.		A	B _I			C			D	D and E			E. is never extreme

TABLE I.—Showing slow, even evolution in the main stock, accompanied by acceleration.

	1	2	3	4	5	6	7	8	9	10	11	12	
<i>V. limopsis</i> . Matthew's Ldg.			A	B _I				C					
<i>V. petrosus</i> . Gregg's Ldg. Race.		A		B _I		C			D and I				E. is very slight.
<i>V. petrosus</i> . Bell's Ldg. Race.		A		B _I		C				D and E			E. is slight.
<i>V. petrosus</i> . Wood's Bluff Race.		A		B _I		C				E and D			E. is extreme.

TABLE II.—Showing senility in an offshoot. The senility increases, not by an acceleration, but by an exaggeration of senile features.

	1	2	3	4	5	6	7	8	9	10	11	12	
<i>V. limopsis.</i> Matthew's Ldg.			A	B _I				C					
<i>V. petrosus.</i> Gregg's Ldg. Race.			A	B _I			C			D and I			E. is very slight.
<i>V. petrosus.</i> Claiborne Race.			A	B _I			C			D and I			I. is great.
<i>V. sayana.</i> Claiborne.			A B _I			C				D and I			D. is much modified. I. is great.

TABLE III.—Evolution of *V. sayana* through the Claiborne race of *V. petrosus*. Shows general acceleration, condensation of B, and reduction in the number of whorls.

	1	2	3	4	5	6	7	8	9	10	11	12	
<i>V. limopsis.</i> Matthew's Ldg.			A	B _I				C					
<i>V. rugatus.</i> Matthew's Ldg.			A	B _I				C			I	E	I. is the transition between C. and E

TABLE IV.—Shows evolution of *V. rugatus* from the primitive ancestral stock by the appearance of senile features in the last whorl or in the last two whorls.

RANGE AND DISTRIBUTION.

Of the forms considered in this paper *Volutilithes limopsis* stands out distinctly as fulfilling all the requirements of an ancestor. Among other characters, the long smooth stage and the absence of senile features show its primitive state. The general likeness of the full-grown shells to the young of many later species, together with its low geological position, justifies us in considering it to be the form from which were descended the races which followed Matthew's Landing time.

In the same horizon with *V. limopsis* we find *V. rugatus*. The young of the latter show many of the features of the adult *V. limopsis*, while the old individuals are often slightly senile and quite different in appearance from the small specimens. It was undoubtedly derived from *V. limopsis*, or some closely allied form, and may be considered a short senile offshoot which did not survive the Matthew's Landing.

In the Nanafalia the first member of the *Volutilithes petrosus* assemblage makes its appearance, and is representative of the *V. petrosus* main stock. After the Nanafalia the races of *V. petrosus* are a prominent feature of the faunas. Though the adults of these races may differ greatly, the young resemble each other closely, and indicate their common derivation from *V. limopsis*.

In the Gregg's Landing marl, the Gregg's Landing race represents the *V. petrosus* main stock, though a few of its individuals show slightly senile tendencies. In the Bell's Landing marl the Bell's Landing race has separated from the main stock with the evolution of senile features. It is the first member of a senile offshoot which in later time produces the Wood's Bluff and Hatchetigbee Bluff races. These latter are evolved from the Bell's Landing race, not so much by an acceleration as by an exaggeration of the marks of senility. The Hatchetigbee Bluff race is without descendants and the last term of this senile series. Its individuals are dwarfed and stunted, reflecting plainly the unfavorable conditions under which they lived, and which soon caused the extinction of the race.

While in some localities the members of the *Volutilithes petrosus* assemblage were following out a line of evolution which resulted in their elimination from the geological record, the main stock was still flourishing in nearby regions. For instance, at Yellow Bluff on the Alabama river we have a representative of the *V. petrosus* main stock. The Yellow Bluff race is indicative of favorable conditions at that locality.

In the Lower Claiborne the *V. petrosus* main stock occurs, though it is represented only by a few poorly preserved specimens. The Claiborne, however, not only gives us the Claiborne race but an offshoot from it, namely, *V. sayana*. This Claiborne race is an assemblage of rather accelerated and variable forms which probably express the effect of shallow water marine conditions upon the main stock. By an acceleration of ornamental features *V. sayana* was derived either from the Claiborne race or from some very closely related form.

Passing now into the Jackson, we find the last member of this phylogenetic series which we have traced up from the Matthew's Landing horizon. It is the Jackson race of *V. petrosus*. This form is the result of the slow and even evolution of the ancestral race which took place in the favorable conditions of a more open sea. Its ontogeny is normal, each stage following its predecessor in regular fashion. Though this form is accelerated, there is little mingling of the senile and spiny characters by unequal acceleration. The senile stage closes a well-

developed spiny stage. This race of *V. petrosus* differs but slightly from the form which we saw in the Nanafalia beds, and demonstrates clearly how little a stock may vary through a long period of time if it is living under favorable conditions.¹²

The phylogeny of the Alabama and Mississippi species of *Volutilithes* may be represented by the table on p. 74. The Yellow Bluff race is provisionally placed in the Bell's Landing horizon.

SUMMARY.

From the Matthew's Landing to the Hatchetigbee inclusive the strata belong to the so-called Lignitic formation. They consist of thick deposits of cross-bedded sands and clays, often glauconitic, and of lignites alternating with thin beds of marine fossils.¹³ It is evident that these deposits were formed in a great shallow arm of the sea, whose waters were sometimes fresh or blackish and at others salt.

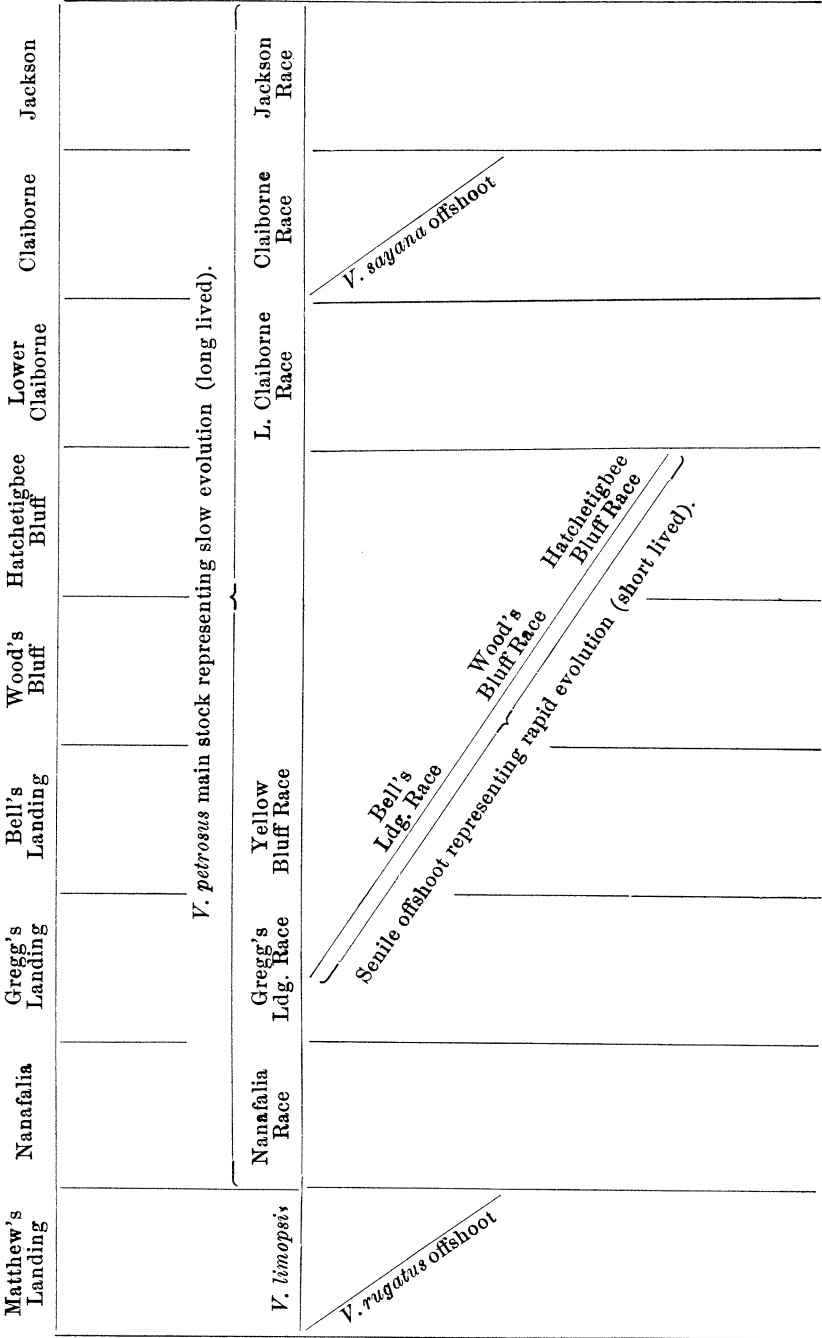
The marine faunas which from time to time invaded this Lignitic gulf brought with them, at first, species and races of *Volutilithes* with normal aspect. These, however, only represent the dwellers on the edge of the respective *Volutilithes* communities, the centres of which were farther out in the open sea. These forms which were subjected to the conditions of the Lignitic eventually followed out a course of evolution which was a direct reflection of their unfavorable environment. The races of *Volutilithes petrosus* at Bell's Landing, Wood's Bluff, and Hatchetigbee Bluff make such a series, in which the senility becomes more and more extreme with the course of time.¹⁴

Occasionally throughout the later Lignitic, as at Yellow Bluff, we find a race which has migrated from a more favorable environment, and which resembles the primitive races of earlier Lignitic waters, as those of Gregg's Landing and Nanafalia. The grade of phylogenetic development which the Yellow Bluff assemblage has attained also

¹² The author has seen forms purporting to come from the Vicksburg horizon which appear to be poorly preserved examples of the Jackson race of *V. petrosus*. He does not, however, feel justified (without further evidence) in carrying the range of *V. petrosus* above the Jackson horizon.

¹³ *Bull. 43, U. S. G. S.*, "Tertiary and Cretaceous Strata of the Tuscaloosa, Tombigbee, and Alabama Rivers," Eugene A. Smith and Lawrence C. Johnson.

¹⁴ It is to be noted in this connection that forms occur in the Miocene of Europe which appear to belong to *Volutilithes* and to possess the shelly overgrowth. The abnormal American races are produced by local conditions, that is, by those of the Lignitic, and are widely separated not only geographically but geologically from the European specimens. It is therefore highly improbable that the European forms (if they are *Volutilithes* at all) are descended from the American ones. In the absence of more definite information, we are justified in regarding the phenomenon as one of parallelism.



indicates that a normal, slow, and even evolution has been going on in one locality; while at the same time rapid, senile evolution has taken place among forms subjected to unfavorable conditions in another region.

Where, then, was the centre of this normal phylogeny? We may well look toward the open sea to find this favorable environment, and the deposits which follow the Hatchetigbee beds furnish us with the desired answer.

With the inauguration of the Lower Claiborne began that movement which finally resulted in the deepening of the sea and the production of the white limestone of the Jackson. The brackish water conditions disappear and are replaced by those of a shallow water (but typically marine) environment. The Claiborne race of *Volutilithes petrosus* shows the effect of such conditions upon the main stock. The sinking of the sea-bottom proceeded throughout Claiborne time, and finally the Jackson limestone with its relatively deep water fauna is introduced. The Jackson race of *V. petrosus* represents the result upon the main stock of slow and even evolution in a favorable environment.

It follows, then, that every stock has some particular set of conditions in which it develops normally. Contemporaneously with this normal phylogeny a senile evolution in the same stock may occur at some less favored locality. In the forms we have considered the environment most favorable to a slow and even evolution is an open sea one, in which limy deposits are forming. It is only, then, in a thick limestone deposit that we could expect to find all the phylogenetic stages of the *Volutilithes petrosus* main stock and other primitive species. In conclusion it is interesting to note that one of the only two existing species of the genus, namely, *Volutilithes abyssicola* Adams and Reeve,¹⁵ is a cancellated form which apparently is quite close in its grade of evolutionary development to the ancestral *V. limopsis* of remote Eocene time. This recent species is found in relatively deep water off the Cape of Good Hope, and probably is a member of a primitive stock, which in the favorable environment of a deep and open sea has been able to persist long after its nearest relatives have become extinct.¹⁶

The writer wishes to express his indebtedness to Prof. Henry A. Pilsbry, of the Academy of Natural Sciences of Philadelphia, and to Prof. Amos P. Brown, of the University of Pennsylvania, for many

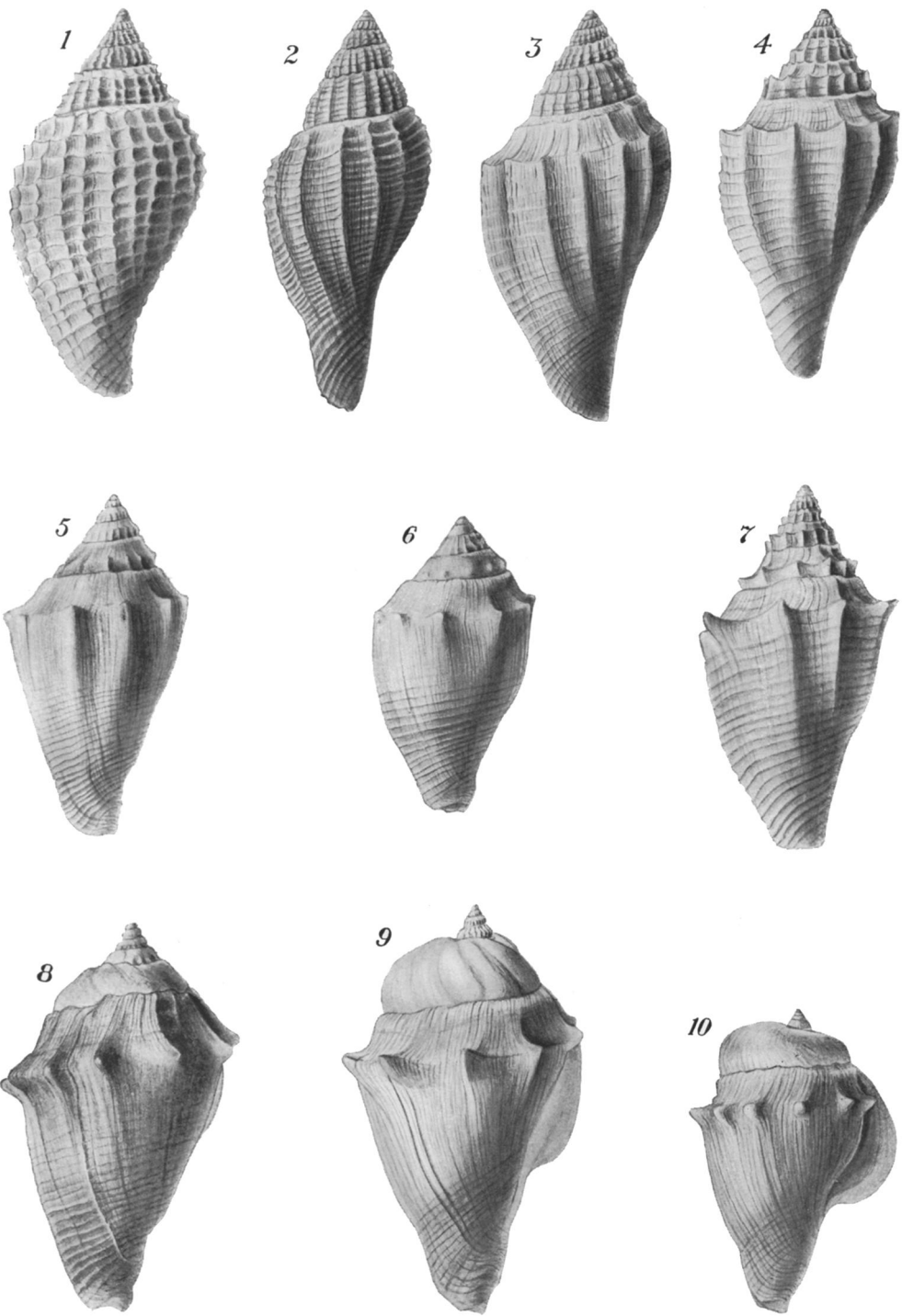
¹⁵ *Zoology of the Voyage of the Samarang.*

¹⁶ See Dall, *Trans. Wag. Inst.*, Vol. III, p. 74.

helpful suggestions, and to Miss Helen Winchester for care exercised in making the drawings. In addition the writer wishes to especially acknowledge the kindness of Mr. Charles W. Johnson, of the Boston Society of Natural History, in giving him much valuable information in regard to the range and distribution of the races and species.

EXPLANATION OF PLATE II.

- Fig. 1.—*Volutilithes limopsis* Conrad. Matthew's Landing, Ala. Adult of moderate size showing the persistence of the cancellated stage throughout the later whorls. Length=18.5 mm.
- Fig. 2.—*Volutilithes rugatus* Conrad. Matthew's Landing, Ala. Young individual showing the cancellated stage. With the exception of the last whorl, the sculpture is very much like that of *V. limopsis*. Length=19.5 mm.
- Fig. 3.—*Volutilithes petrosus* Conrad. Bell's Landing Race. Bell's Landing, Ala. Young individual showing the cancellated stage. Length=20 mm.
- Fig. 4.—*Volutilithes petrosus* Conrad. Jackson Race. Jackson, Miss. Young individual showing the cancellated stage. Length=19 mm.
- Fig. 5.—*Volutilithes petrosus* Conrad. Gregg's Landing Race. Gregg's Landing, Ala. Adult individual showing the general characters of the *V. petrosus* main stock. The later whorls show the spiny stage. Length=50 mm.
- Fig. 6.—*Volutilithes petrosus* Conrad. Yellow Bluff Race. Yellow Bluff, Ala. Adult individual showing the general characters of the *V. petrosus* main stock. This is, however, not as typical an expression of the features of the main stock as is seen in fig. 5. The later whorls show the spiny stage. Length=44 mm.
- Fig. 7.—*Volutilithes petrosus* Conrad. Jackson Race. Jackson, Miss. Adult individual showing the general characters of the *V. petrosus* main stock. The later whorls show the spiny stage. This is the culminant type of the main stock. Length=52 mm.
- Fig. 8.—*Volutilithes petrosus* Conrad. Bell's Landing Race. Bell's Landing, Ala. Adult individual showing the slightly developed senile characters. Length=52 mm.
- Fig. 9.—*Volutilithes petrosus* Conrad. Wood's Bluff Race. Wood's Bluff, Ala. Adult individual showing strongly developed senile characters. Length=58 mm.
- Fig. 10.—*Volutilithes petrosus* Conrad. Hatchetigbee Bluff Race. Hatchetigbee Bluff, Ala. Adult individual showing extreme senility and dwarfed size. This is the culminant type of the senile offshoot shown in figs. 8 and 9. Length=43 mm.



BURNETT SMITH. PHYLOGENY OF THE RACES OF
VOLUTILITHES PETROSUS.